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Modeling the krill transport pathways in the Scotia Sea: spatial and environmental connections generating the seasonal distribution of krill

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Abstract

A coupled physical–biological model analysis was undertaken to examine the seasonal development of the distribution of antarctic krill (*Euphausia superba* Dana) in the Scotia Sea. The origin and fate of krill observed during the CCAMLR 2000 survey were studied using output from the OCCAM model. Lagrangian particle tracking for the period prior to the survey showed the expected dominance of the west to east flow of material associated with the main direction of the current flow, but there was no simple association of particle transport with any of the fronts of the Antarctic Circumpolar Current. Most of the krill were associated with areas to the south of the Antarctic Circumpolar Current in the Weddell–Scotia Confluence (WSC) and farther east in Weddell Sea-influenced waters. Examining the pathways of krill transport in relation to satellite-derived sea-ice distributions suggests that particles present in the high krill biomass regions in January would have come from areas that were covered by sea-ice during late winter/early spring (September–October). The results of Eulerian grid-based simulations of the development of the biomass distribution after the survey period showed transport of particles around South Georgia, probably in association with the Southern Antarctic Circumpolar Current Front. However, many of the krill encountered in the eastern Scotia Sea would have exited toward the east, passing north of the South Sandwich Islands, probably in association with the Southern Boundary of the Antarctic Circumpolar Current and Weddell Sea waters that penetrate to the north in this area. These krill may return to more southern regions where further spawning is possible in later years. Simulations of particle tracks that included diurnal vertical migration showed that krill behavior could modify the pathways of transport, although the current flows probably dominate the movement of krill in open ocean regions. This study suggests that the summer distribution of krill in the Scotia Sea is connected to the winter sea-ice distribution and probably to the pattern and rate of the spring sea-ice retreat. Many of the krill in the survey region in the summer of 1999/2000 came from under the sea-ice in the eastern Scotia Sea, the southern Scotia Arc, and the northern Weddell Sea. This highlights that the spatial association of the sea-ice with the Weddell–Scotia Confluence and frontal regions of the Antarctic Circumpolar Current during winter and spring will be crucial in determining the summer krill

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distribution. Variation in the extent and timing of sea-ice retreat, and fluctuations in Weddell–Scotia Confluence and Scotia Sea flows, will change the pathways of transport resulting in large changes in the distribution of the krill during summer.

1. Introduction

The Scotia Sea and surrounding shelf areas contain the most extensive regions of high biomass of Antarctic krill (*Euphausia superba* Dana) in the Southern Ocean (Marr, 1962). The area also includes many of the major predator colonies of the Southern Ocean (Croxall et al., 1988) and is the area where krill fishing has been concentrated (Murphy et al., 1997, 1998). The main sites around the Scotia Sea (Fig. 1) where viable krill spawning occurs are not well known, but are probably in the shelf areas to the east and west of the Antarctic Peninsula (Marr, 1962). The distribution of krill extends far to the north of the Scotia Arc, but stocks of krill in the northern Scotia Sea are probably not self-sustaining, relying on input from areas further south (Marr, 1962; Ward et al., 1990). The krill are a key component of the regional food web, being the major prey item for many of the key predators such as the fur seals and macaroni penguins that occur in large numbers in the Scotia Sea (Croxall et al., 1985). Long-term observations of krill abundance and availability to predators have shown that there is large inter-annual variability in the abundance of krill in the Scotia Sea region that is associated with major changes in the ecosystem (Atkinson et al., 2001; Murphy et al., 1998). Although krill are a key component of the regional ecosystem in the northern Scotia Sea, the major transport routes, the links between these transport routes and winter sea-ice cover, and the sites to which the krill are transported during the late summer period are unknown (Hofmann et al., 1998; Murphy et al., 1998).

Many studies have considered the physical (including spatial links) and biological factors that may be important in generating the observed variation in krill abundance in the Scotia Sea (Murphy and Reid, 2001; Murphy et al., 1998; Priddle et al., 1988). Early studies of the large-scale distribution of krill showed that the surface circulation associated with the West Wind Drift (now termed the Antarctic Circumpolar Current—ACC) and the Weddell–Scotia Confluence (WSC) was important in generating the observed distribution of krill in the Scotia Sea (Marr, 1962). Priddle et al. (1988) discussed how fluctuations in ocean frontal positions as a result of changes in atmospheric circulation patterns could influence the distribution and transport of krill. Subsequently, the fluctuations in krill abundance were related to coherent changes in the coupled atmosphere-ice-ocean systems of the Southern Ocean (Fedulov et al., 1996; Murphy et al., 1995). More recently, as understanding of the dynamics of krill populations has increased, Murphy and Reid (2001) showed that fluctuations in year-class strength of krill are also an important component of the observed variation. Understanding the geographical, winter–summer connections in the development of krill distributions in the Scotia Sea is fundamental to determining what generates the observed variation and to predicting the response of these systems to change.

Marr (1962) and Mackintosh (1973) considered that krill could enter the Scotia Sea in two ways; through Drake Passage past the Antarctic Peninsula in the ACC or from the east of the Antarctic Peninsula associated with the surface outflow in the WSC or northern penetrations of the Weddell Gyre. Thus, krill at South Georgia could come from these two apparently distinct regions, and there have been suggestions that the different types of krill observed in the area have their origin in these different regions (Mackintosh, 1973; Watkins et al., 1999). The frontal regions of the ACC also are thought to have an important role in the transport of krill in the Scotia Sea (Hofmann et al., 1998; Murphy et al., 1998). As these fronts are routes of enhanced current speed, it is suggested

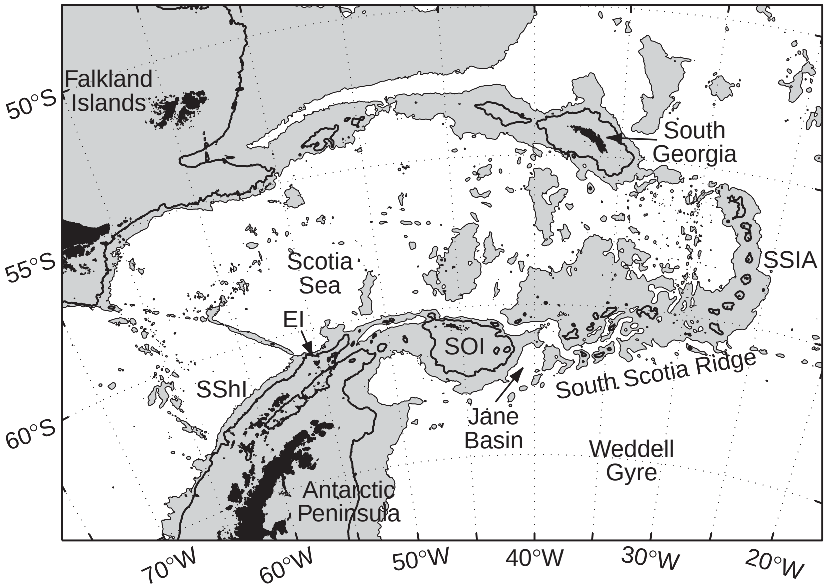

Fig. 1. Bathymetry of the study region: areas shallower than 3000 m are shaded gray and the 1000 m isobath is shown. Abbreviations marked are EI—Elephant Island, SShi—South Shetland Islands, SSIA—South Sandwich Island Arc, SOI—South Orkney Islands.

that flows from the Antarctic Peninsula region are the main route for bringing krill into the northern region of the Scotia Sea around South Georgia.

Much of the study of krill distribution has been based on data collected during summer months when most of the region is free of sea-ice, so there is a tendency to concentrate on the ocean flows and connections to frontal regions when considering the major factors influencing distribution (Hofmann et al., 1998; Murphy et al., 1998). The sea-ice environment is known to be crucial to krill in the Scotia Sea; Marr (1962) and Mackintosh (1973) both emphasized that the large-scale distribution of krill during summer was related to the sea-ice retreat in spring, and it has long been known that the marginal ice regions are areas of high krill abundance. Much of the harvesting of the great whales occurred in the marginal ice regions where they were observed to be feeding on krill. Murphy et al. (1998) discussed the potential for variability in sea-ice extent (Murphy et al., 1995) to change the interaction of the sea-ice with the flow field during spring and thus to modify the summer krill distribution. Recently, Fach et al. (2002) showed how interaction with the sea-ice environment may be a key aspect in krill survival during transport in the Scotia Sea.

It also has been suggested that active movement of krill may be important in the development of the large-scale distribution. Krill are known to be strong swimmers and in many ways are more similar to small fish than plankton. Krill have been recorded swimming at rates of 40–50 $cm\,s^{-1}$, but such rates are considered an escape response and cannot be maintained for extended periods (Kils, 1981). In shallow coastal regions, or in areas of sea-ice and icebergs, krill are able to undertake directed swimming in relation to small-scale (1–10 m) environmental cues (Marr, 1962, p. 434). In coastal regions of the Antarctic Peninsula active migration has been identified as a likely mechanism for the movement of krill from shallow to deeper waters (Siegel, 1988; Trathan et al., 1993), and in such areas active krill movement may be important in the horizontal transport of krill. In more open-ocean regions such as the central Scotia Sea, where the flow rates are consistent and high ($>$10–15 $cm\,s^{-1}$) compared to the mean swimming speeds of krill (6–13 $cm\,s^{-1}$), it is difficult to envisage a situation in which active migration will be important (Marr, 1962, pp. 416–421 and 434). Although there will be a small-scale response to local stimuli, for this to be significant in the broad scale transport would require a consistently directed migration in deep-water areas in response to a large-scale external stimulus. Although such possibilities have been discussed, there is no evidence to support this speculation (Marr, 1962, p. 229). Vertical migration is a different matter and may have an effect depending on the vertical shear structure of the flow field (Hardy, 1967). Ekman-drift generated variations in vertical flow produce vertical shear in the velocity field. Such differential movement of surface and deeper currents may allow vertical migration effects to produce differences in the pathways of transport (Murphy et al., 2004; Tarling et al., 2000). Horizontal shear effects occur as a result of differential flow rates in ocean currents as is observed between the major fronts of the ACC (Orsi et al., 1995). For there to be any behavioral effect the krill would need to undertake a directed response in relation to the flow, which would require some form of response to the larger-scale gradient in flow. The simplest assumption at this stage is that the krill can respond to small-scale cues, which may affect the large-scale distribution generated, but there is no evidence that they undertake a large-scale directed migration in open waters.

Most of the studies of spatial connection in the Scotia Sea are based on general observations of krill occurrence in the southern Scotia Sea and at South Georgia and not on the broader distribution. The only large-scale view available is from the *Discovery* expeditions during the first half of the 20th century (Marr, 1962). The CCAMLR 2000 Survey (a multi-national, multi-ship survey during the austral summer of 2000 to estimate the biomass and distribution of Antarctic krill in Area 48), therefore provides the most comprehensive and up to date view available of the large-scale distribution of krill in the Scotia Sea over a short period of time (Hewitt et al., 2004; Watkins et al., 2004). The CCAMLR 2000 Survey data provide a unique opportunity to consider the development and fate of the krill in ocean currents in the Scotia Sea. Until recently there have been limited particle tracking analyses based on climatological analyses of flow fields or using a mean field analysis from a General Circulation Model for the region (Hofmann et al., 1998; Murphy et al., 1998). Model output generated using realistic, temporally varying, wind fields derived from model analysis of observations is now becoming available. This makes it possible to consider temporal variability (Thorpe et al., 2002, 2004a) and the particular flow conditions during the period of field observations. However, the current models do not include realistic simulations of sea-ice dynamics, but the availability of detailed satellite data means that seasonal variations in sea-ice extent can be analyzed in conjunction with the modeled flow fields. The combination of realistic time-varying sea-ice fields with modeled ocean-flow fields for the same period, coupled with the large-scale view of krill distribution, gives the potential to develop analyses of the seasonal, spatial, and environmental connections controlling the dynamics of krill distributions.

This paper reports on a modeling analysis of the potential pathways of transport and the development of the krill distribution in the Scotia Sea. The aims of this study were: (i) to develop Lagrangian particle track analyses of the pathways of transport during the austral spring (September–December) for krill that were observed in the high biomass regions during January, (ii) to develop an Eulerian simulation of the dynamic development of the krill biomass field in the period following the survey (January–April) to investigate the fate of the krill, and (iii) to examine the potential for behavioral vertical migration effects to modify the pathways of krill transport.

2. Methods, models, and data

2.1. Krill biomass distribution

The multi-national CCAMLR 2000 Survey took place during January and February 2000. Each of the four participating ships collected calibrated comparable acoustic data, together with key biological and environmental data collected according to a set of strict protocols along 22 major transects that covered the likely distribution range of krill, i.e. 20–70°W (Watkins et al., 2004). The combined data set from the four ships was used to estimate the acoustic biomass of krill (SC-CAMLR, 2000). The depth-integrated biomass field generated from these analyses (Hewitt et al., 2004) is used to analyze the effects of current flow (Fig. 2). The krill biomass data were 0.5° latitude by 1° longitude resolution and were regridded at 0.25° resolution for coupled analyses with the velocity data.

2.2. Model velocity fields

Output from the 6-hourly wind forced run of the Ocean Circulation and Climate Advanced Modelling Project (OCCAM) model (Saunders et al., 1999; Webb and de Cuevas, 2003; Webb et al., 1998) is used to provide the velocity fields for the particle tracking and grid-based models (Fig. 3). OCCAM is a global, eddy-permitting z level primitive equation model of the Bryan–Cox–Semtner type and includes a free surface (Killworth et al., 1991). It has a horizontal resolution of $0.25° \times 0.25°$ with 36 vertical levels ranging in thickness from 20 m at the surface to 255 m at depth. The model bathymetry is derived from the DBDB5 data set (Anon, 1983), with manual checking and correction where necessary of key sills (Thompson, 1995). The model has been run over the period 1992–2000, forced with the European Centre for Medium-Range Weather Forecasts' 6-hourly reanalyzed wind data set and relaxed to climatological (Levitus and Boyer, 1994; Levitus et al., 1994) temperature and salinity values to provide the surface heat and freshwater forcing. Monthly mean velocity fields are used in this work to eliminate aliasing of inertial oscillations that occur when models are forced with high frequency wind stress and the output is sampled as snapshots (Jayne and Tokmakian, 1997).

2.3. Particle tracking

To assess the likely origins of the regions of high krill biomass in the CCAMLR 2000 Survey data, a Lagrangian particle tracking method is used. Transport of passive drifters released on a regular grid covering the Scotia Sea (Fig. 4) is simulated using a two-dimensional Runge–Kutta advection scheme. The position of a particle at timestep $n+1\,[\mathbf{x}_{n+1} = (x_{n+1}, y_{n+1})]$ is given by

$$\mathbf{x}_{n+1} = \mathbf{x}_n + \mathbf{v}_{n+\frac{1}{2}}\Delta t, \tag{1}$$

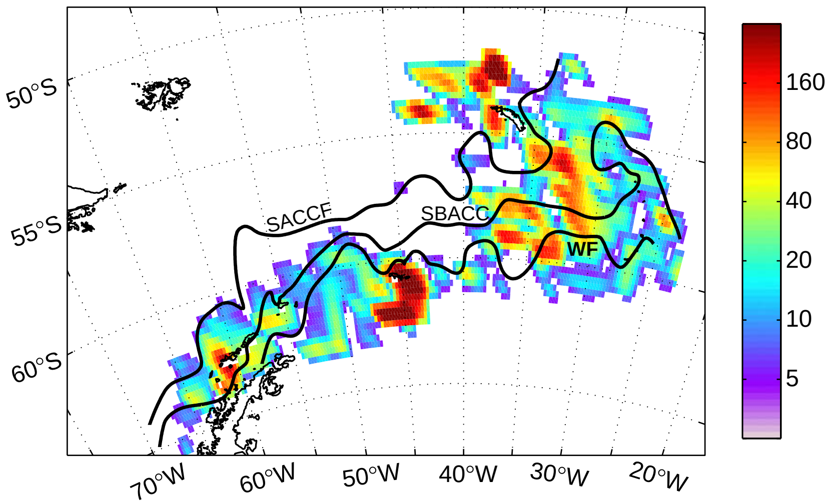

Fig. 2. The distribution of integrated krill biomass (g m^{-2}) generated by the CCAMLR 2000 Survey, January–February 2000 (Hewitt et al., 2004). The positions of the Southern Antarctic Circumpolar Current Front (SACCF), the Southern Boundary of the Antarctic Circumpolar Current (SBACC), and the Weddell Front (WF) are as identified by Brandon et al. (2004).

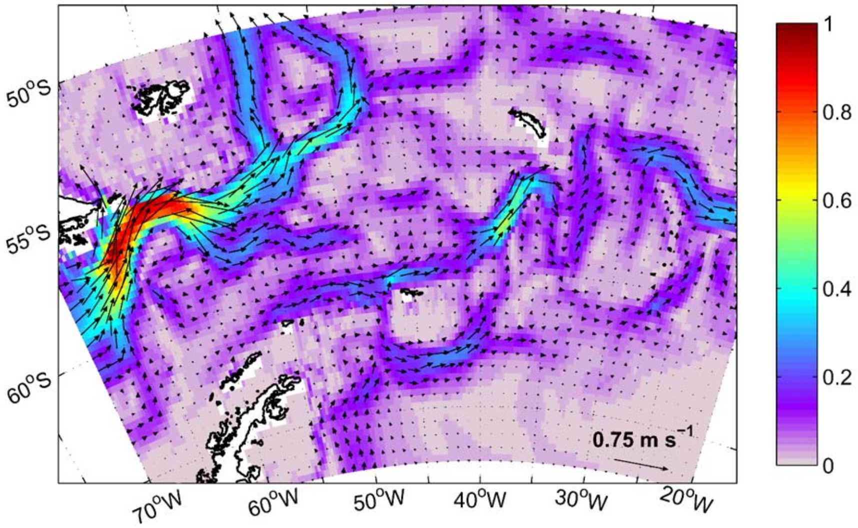

Fig. 3. Six-month average of the depth-weighted mean velocity fields for the upper 182 m (levels 1–7) of OCCAM in the Scotia Sea for October 1999–March 2000. Colors show magnitude, arrows (not shown at every grid point for clarity) have been capped at 0.75 m s^{-1}.

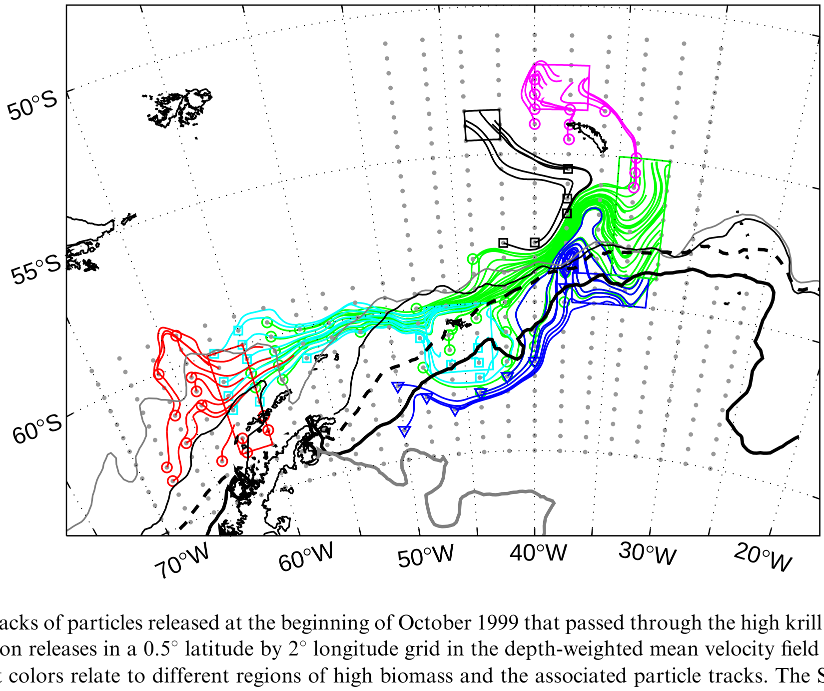

Fig. 4. Lagrangian tracks of particles released at the beginning of October 1999 that passed through the high krill biomass areas during January 2000. Based on releases in a 0.5° latitude by 2° longitude grid in the depth-weighted mean velocity field over the upper 182 m (levels 1–7). Different colors relate to different regions of high biomass and the associated particle tracks. The September to January ice-edge (15% concentration) positions are also shown (September 1999 thin gray line; October 1999 solid black line; November 1999 broken black line; December 1999 thick black line; January 2000 thick gray line).

where $\mathbf{x}_n = (x_n, y_n)$ represents the position of the particle at the previous timestep n and Δt is the timestep. The advection scheme is second-order accurate. The particle is advected with velocity $v_{n+\frac{1}{2}} = (u_{n+\frac{1}{2}}, v_{n+\frac{1}{2}})$. This is the component of velocity at the particle's predicted position at time $n+\frac{1}{2}\Delta t$ (i.e. at position $\mathbf{x}_{n+\frac{1}{2}}$, where $\mathbf{x}_{n+\frac{1}{2}} = \mathbf{x}_n + \frac{1}{2}\Delta t \cdot \mathbf{v}_n$). To satisfy stability criteria, $\Delta t = 0.1$ days for the scheme, which thus requires interpolation between the monthly mean velocity fields from OCCAM. Prior to this interpolation, the mean monthly velocity fields are modified following the method of Killworth (1996) to avoid errors associated with straightforward linear interpolation between monthly means. Depth-weighted mean fields for each month are calculated over the upper five, seven and ten levels of the model (the upper 116, 182 and 323 m of the model's water column, respectively). The consecutive fields are used in the particle tracking. A no-slip condition is in place at land areas, and once particles have left the model domain they take no further part in the simulation.

2.4. Grid-based model

To simulate the temporal development of the krill biomass field determined by Hewitt et al. (2004) an Eulerian advection model is used in which the movement of the entire biomass distribution field is simulated at each timestep. As with the particle tracking scheme, the advection model uses the consecutive monthly mean velocity fields from the 6-hourly wind forced run of OCCAM, modified according to Killworth (1996) for the effects of linear interpolation. Advection is modeled with a forward time-stepping scheme using the multidimensional positive definite advection transport algorithm (MPDATA) of Smolarkiewicz (1984), modified according to Smolarkiewicz and Clark (1986) for time-dependent velocity fields. The MPDATA scheme has small implicit diffusion and is based on an iterative application of the upstream scheme. In the first iteration, the velocity data from OCCAM are used to define the fluxes between grid cells in the upstream scheme. To compensate for truncation errors that are introduced into the original scheme when using time-dependent velocity fields, the velocity data used in this first iteration are interpolated to the $n+\frac{1}{2}\Delta t$ timestep following Smolarkiewicz and Clark (1986). Each subsequent 'corrective' iteration reapplies the upstream scheme using 'antidiffusive' velocities calculated to reverse the diffusion process implicit in the upstream scheme. The accuracy of the MPDATA method increases with the number of iterations applied; here three iterations are used and these give sufficient accuracy. To satisfy stability criteria, a time-step of $\frac{1}{12}$ day is applied. The biomass distribution is assumed to be representative of mid-January and is developed over time using the advection scheme with the consecutive modified mean monthly velocity fields linearly interpolated in time. A no-slip condition is set for land areas so that there is no flux onto land. Fluxes out of the model domain take no further part in the simulations and there is no influx of biomass to the model.

The MPDATA scheme can be extended to include diffusion (Smolarkiewicz and Clark, 1986). However, simulations performed using the advection–diffusion scheme with positive diffusive fluxes give the same general distribution features in the biomass distribution field as the advection only scheme described in the previous paragraph and thus the results from the advection–diffusion algorithm are not presented here.

2.5. OCCAM representation of flow fields in the Scotia Sea

OCCAM gives a good representation of the general circulation field in the Scotia Sea; however, a comparison of the positions of the ACC fronts generated in OCCAM indicates that between 60° and 40°W the fronts are further south than expected (Fig. 2; Brandon et al., 2004; Thorpe et al., 2004b). Farther east the model reproduces well the general positions of the fronts (Brandon et al., 2004; Orsi et al., 1995). Brandon et al. (2004) show that the WSC is observed in the CCAMLR 2000 Survey data penetrating east from the Antarctic Peninsula shelf regions as far as the South Orkney Islands. Beyond the South Orkney Islands the WSC signal disappears and Weddell Sea waters penetrate north around the South Sandwich Islands (Fig. 2; Brandon et al., 2004).

3. Results

3.1. Lagrangian particle tracking

The krill biomass distribution across the Scotia Sea during the CCAMLR 2000 Survey was highly heterogeneous, with more than 50% of the biomass concentrated into six meso-scale ($\sim$400–700 km^2) areas of high-biomass ($>100\,\mathrm{g\,m^{-2}}$). The particle tracking analyses undertaken here focus on the transport of the krill into these six high biomass regions. These regions of high biomass occurred in the vicinity of the South Shetland Islands from the on-shelf region northward toward deeper waters, around the shelf region of the South Orkney Islands, across the central Scotia Sea at about 30–40°W, and north and west of South Georgia (Fig. 2; and outlined for modeling purposes by colored boxes in Fig. 4). Analyses of a gridded set of releases starting in October 1999 showed those particles that would have passed through the high biomass regions during January 2000 (Fig. 4). Analyses based on depth-weighted mean velocity fields for the upper 116, 182, and 323 m (model levels 1–5, 1–7, and 1–10, respectively) showed very similar results (Fig. 5). Calculated mean, minimum, and maximum values for transport of particles across different regions are given in Table 1. The size of the boxes over which these calculations are made make a big difference to the derived values, as shown for the two regions at the South Orkney Islands. In this area there is the potential for very slow flow rates associated with the shallow shelf regions retaining particles and generating long transport times.

The simulations show that particles in the high biomass regions during January were generally moved from the west in the main flow of the ACC and WSC (Figs. 2–4). Examination of the transport pathway analyses with data on the monthly sea-ice extent from September shows that except for the most northern regions, to the west of South Georgia, the particles transported into the areas of high krill biomass would have been in areas covered by sea-ice approximately 2–3 months before the survey (Figs. 4 and 5; see also Table 1). Particles in the southeastern regions of the Scotia Sea and around the South Orkney Islands were in areas covered by sea-ice as late as November or December (Figs. 4 and 5). This is consistent with the oceanographic data analyses that show a relatively freshwater lens of water at the surface in areas in the southeastern Scotia Sea that was probably derived from recent ice-melt associated with sea-ice cover (Brandon et al., 2004). The simulations indicate that particles in the high biomass regions around the Antarctic Peninsula (60–62°W) were brought into the region either in the ACC from the west or were transported north and east on the shelf (Figs. 4 and 5).

To the east of the Antarctic Peninsula along the Scotia Arc the circulation field connects the main high biomass regions (Figs. 3 and 4). The focused nature of the flow trajectories indicates that these flows are associated with frontal regions. Particles in the region of the South Shetland Islands, west of 60°W, that were exposed by the retreating sea-ice in about October–November were transported east and reach the South Orkney Islands by about January (Figs. 4 and 5, pale blue lines and symbols; mean transport times of 84–101 days, Table 1). Right across this region, from the Antarctic Peninsula at 60°W to about 40°W, particles were transported to the east to pass through the high biomass regions in the eastern Scotia Sea during January (Figs. 4 and 5, green lines and symbols). Particles further east of about 60°W in about October were transported more rapidly to the east reaching the central Scotia Sea around 35°W by about January (Figs. 4 and 5, dark blue lines and symbols). Particles in the central Scotia Sea during October were transported north to occur around the western end of South Georgia during January (Figs. 4 and 5, black lines; mean transport times from the South Orkney Islands to South Georgia of 76–89 days, Table 1). One or two months previously, during June or July, these particles would have been in the vicinity of the ice edge to the west of the South Orkney Islands (Figs. 4 and 5). These flow routes along the north side of the Scotia Arc and across the Scotia Sea reflect the major pathway of flow of the ACC/WSC where the Southern Antarctic Circumpolar Current Front (SACCF), the

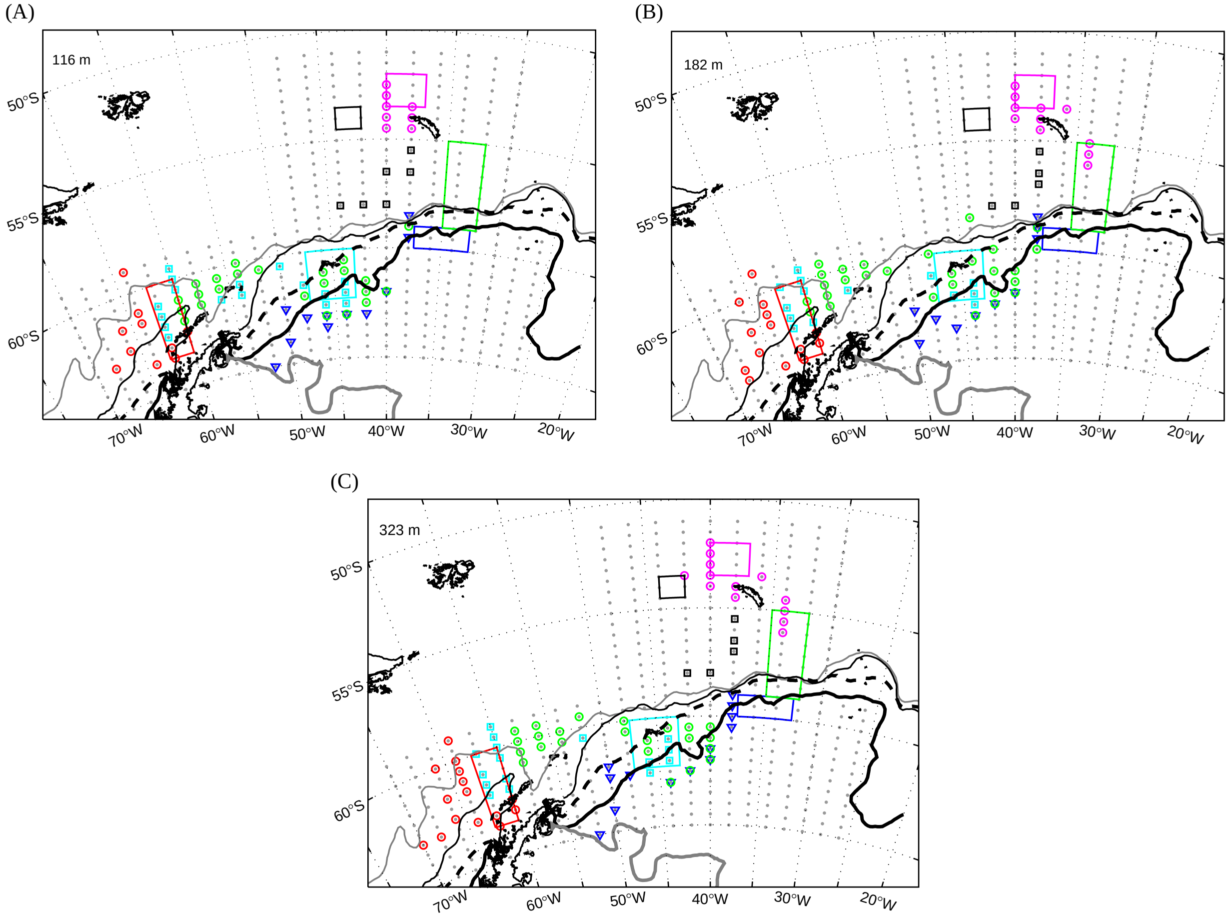

Fig. 5. Starting positions in a 0.5° latitude by 2° longitude grid for passive particles released at the start of October 1999 that pass through the main areas of high biomass observed during the CCAMLR 2000 Survey in January 2000. Panels show particles released in the depth-weighted mean velocity field for (A) the upper 116 m (levels 1–5), (B) the upper 182 m (levels 1–7), and (C) the upper 323 m (levels 1–10). The September to January ice-edge positions are also shown (see Fig. 4).

Southern Boundary of the Antarctic Circumpolar Current (SBACC), and the WSC occur close together (Figs. 2, 4 and 5; Brandon et al., 2004). The eastward and northward trajectories of particle transport may have been mainly associated with frontal regions but it is not possible to distinguish the dominance of a particular front in the transport of krill in this analysis.

Particles present in the more southern regions of the Scotia Sea at about 60°S and 35°W and on the southern shelf at the South Orkney Islands would have been under the ice until late November or December and would have been transported in the WSC along the southern side of the Scotia Arc through Jane Basin or out of the Weddell Sea (Figs. 1, 4 and 5; dark blue symbols and lines).

3.2. Larval krill distribution

Most of the larval krill observed across a large area of the Scotia Sea north of about 60°S were calyptopis stages 1 and 2 (>70%; Siegel et al., 2004) and about 30–45 days old (Siegel et al., 2004; Ward et al., 2004). During the development phase these larvae would have gone through a descent–ascent cycle associated with egg sinking

Table 1
The mean, minimum, and maximum time (days) for the transport of passive drifters between regions

Start area	End area	Depth (m)	Number of release grid points	Number of arrivals	Transport time (days)		
					Mean	Min	Max
Antarctic Peninsula	South Orkneys 1	116	16	10	93	60	126
		182	16	11	98	65	132
		323	16	11	101	72	125
	South Orkneys 2	116	16	11	84	52	118
		182	16	11	88	56	115
		323	16	11	89	62	115
	South Georgia	116	16	11	162	74	227
		182	16	11	159	74	202
		323	16	11	158	74	198
South Orkneys 1	South Georgia	116	10	3	76	61	101
		182	10	3	79	67	101
		323	10	3	88	74	101
South Orkneys 2	South Georgia	116	45	7	82	61	114
		182	45	7	84	67	111
		323	45	7	89	71	103

Releases were made at fixed grid points shown in Fig. 4 and the number of those releases arriving in different regions is also shown. Three scenarios are shown for each of the regions based on the depth-weighted mean current fields over 116, 182, and 323 m. Areas were defined as follows: Antarctic Peninsula: 60–62.5°W, 60–63.5°S; South Orkneys 1: 43–47.5°W, 60–62.25°S; South Orkneys 2: 42–50°W, 60–64°S; South Georgia: 32.5–45°W, 52–55°S.

and larval ascent over about 1000 m (Capella et al., 1992). While not modeled explicitly, the short duration of the vertical cycle (about 10–20 days) and the general consistency of flow direction between about 100 and 1000 m mean that upper water column (<250 m) particle tracking will give a reasonable representation of the general flow direction although distances may be overestimated. Particle tracking indicates that the larvae were transported into the region where they were observed in January from the west in association with the ACC (Figs. 2 and 6). Thus the krill larvae in these more northern regions were probably from areas on the northern side of the Scotia Arc associated with the ACC, probably flowing through Drake Passage from the offshore regions near the Antarctic Peninsula. These were areas where sea-ice occurred two to three months prior to the survey so the larvae were probably produced during November to December in open waters revealed by the retreating ice edge between about 65° and 55°W (Fig. 6). On the basis of the particle tracking, some of the krill larvae in the more eastern regions will have come from areas further south in the WSC that were covered by ice until late October or into November (Fig. 6) while some were probably never under the ice. However, the Lagrangian analyses indicate that the krill larvae observed in the most southerly regions during January (south of 60°S) were under the ice in the WSC and northern Weddell Sea until late November or December (Fig. 6).

3.3. Forward projections of the biomass distribution

In this section references to krill transport concern the modeled krill biomass field. Eulerian projections of the krill biomass field showed that passive drifters in the shelf regions near the South Shetland Islands, the South Orkney Islands, and to a lesser extent around South Georgia, would have been retained for extended periods in these areas because of low flow rates and complex flow patterns. The results from the simulations show

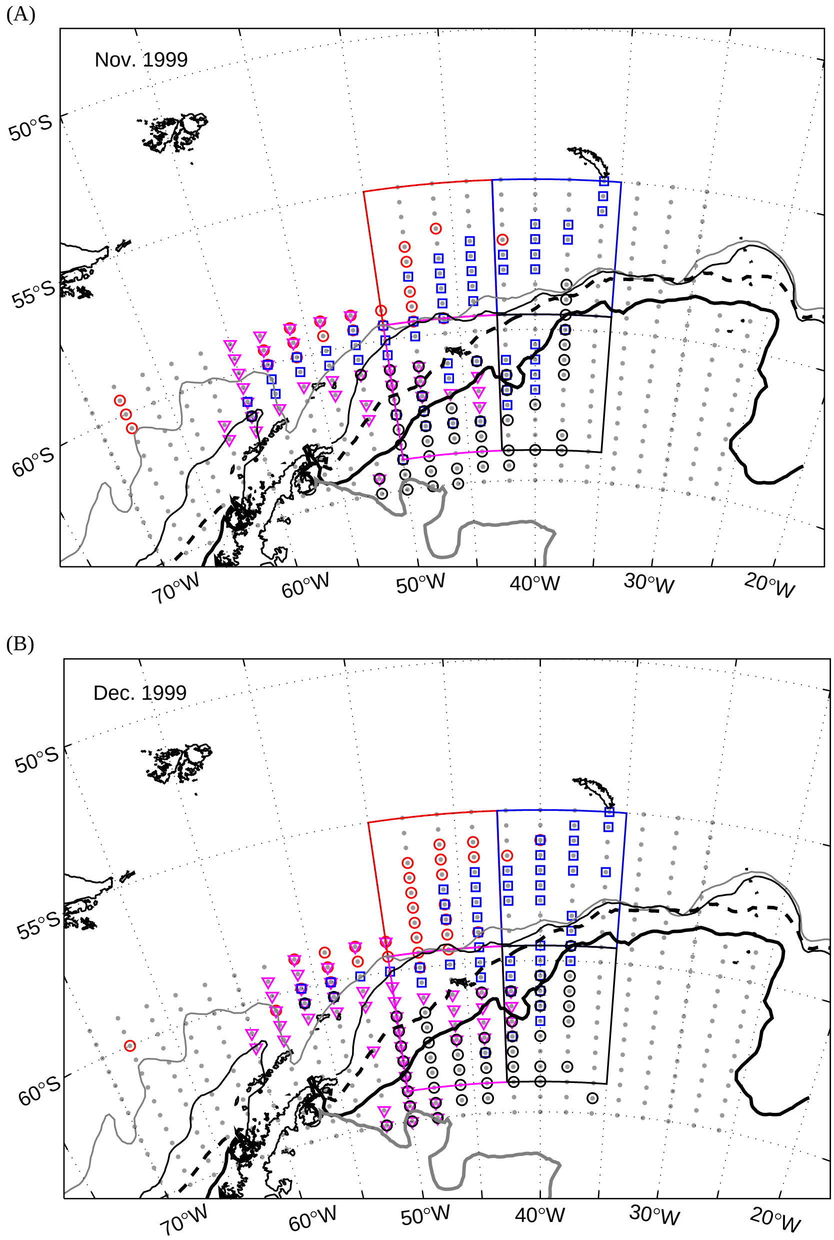

Fig. 6. Starting positions in a 0.5° latitude by 2° longitude grid for passive particles released at the start of November and December 1999 that pass through the regions where krill larvae were observed during the CCAMLR 2000 Survey during January 2000. All plots were based on the depth-weighted mean velocity field for the upper 116 m at the start of: (A) November and (B) December. The September–January ice-edge positions are also shown (see Fig. 4).

that krill in these more inshore areas were relatively static during the three months after the survey (Fig. 7). The flow in these regions will not have been fully represented in the OCCAM resolution data, but retention in these areas is supported by drifter data.

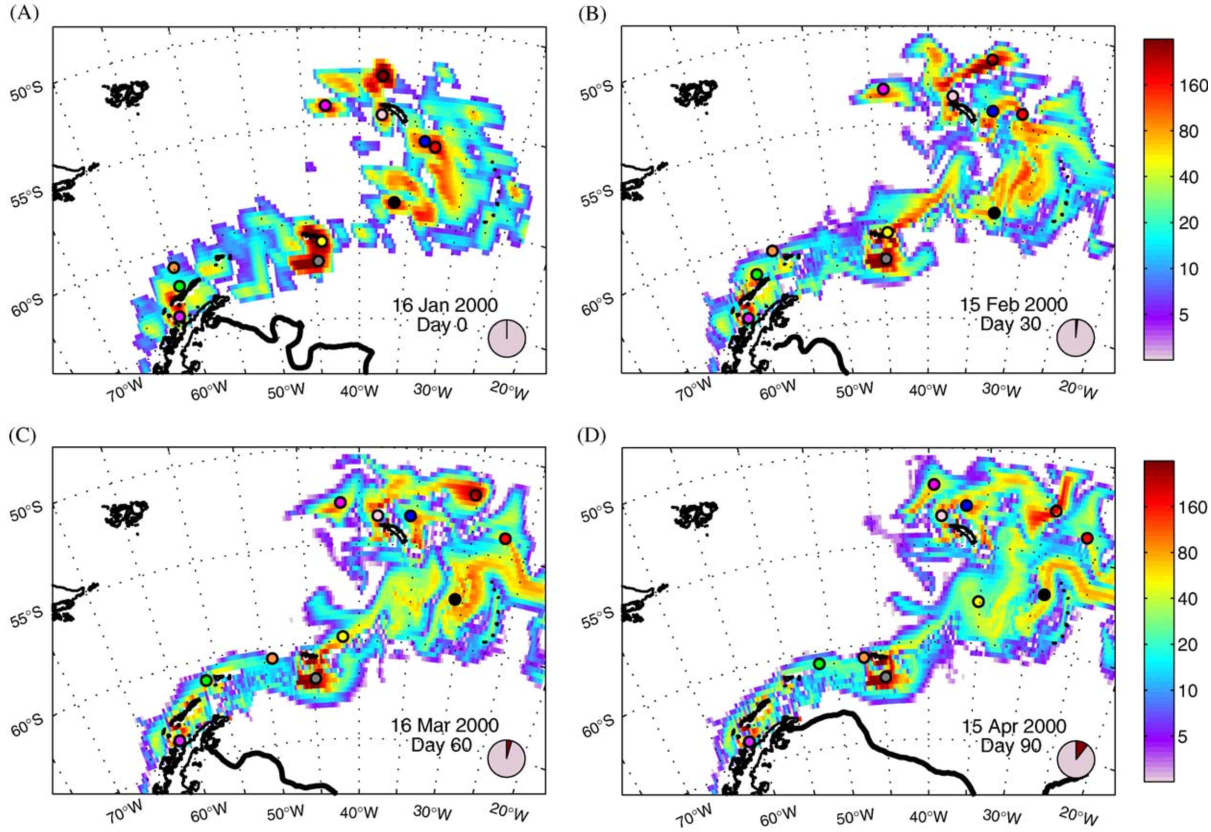

Fig. 7. The time-evolving krill biomass distribution based on the CCAMLR 2000 Survey krill field (Hewitt et al., 2004) and the OCCAM velocity fields (depth-weighted mean for the upper 182 m) for the three-month period following the CCAMLR 2000 Survey in January. The krill biomass ($g\,m^{-2}$) field is shown for: (A) day 0 (original grid), (B) day 30, (C) day 60, and (D) day 90. The colored points show the position of passive drifters released on 16 January 2000 on each of these days. Thick black lines mark the mean ice edge (15% concentration) for each month. The circular pie chart shows the proportion of the original krill biomass remaining in the grid area.

The simulations show modeled krill biomass from the high biomass regions streaming downstream as the projection progresses (Fig. 7). Krill biomass can be transported from the South Shetland Islands to the South Orkneys in around two to three months (Table 1). By about the end of March, when sea-ice was advancing northward, krill from the Antarctic Peninsula would have reached the South Orkney Islands. Krill from the northern side of the South Orkney Islands were transported across the Scotia Sea, reaching the central Scotia Sea in about three months (Fig. 7). These flows from the Antarctic Peninsula and the South Orkney Islands will have been associated with the major route of flow of the ACC and WSC. However, it is not possible to distinguish whether there is one main route of krill transport associated with a particular front in this area using these model runs. This is a complex zone where the fronts and water masses are close together, are not well defined in the surface waters, and are highly dynamic with much mixing. This is illustrated in the simulations, which show that flow routes in the eastern Scotia Sea are very sensitive to the initial positions of the krill (Fig. 7). This is not the WSC region, which is known to be a highly variable eddy region (e.g., Bogdanov et al., 1969; Deacon, 1933, 1937; Foster and Middleton, 1984; Maslennikov and Solyankin, 1979), but the area across the SACCF and SBACC to the north of the region where the surface signature of the WSC has disappeared. Krill farther west (~35°W between ~55° and 58°S, e.g., blue marker Fig. 7) were transported along the route of the SACCF to the north and then west around South Georgia. Krill just to the east of this region (e.g., red marker Fig. 7) were entrained in the main flow associated with the SBACC and taken to the north and then east around the north of the South Sandwich Islands at about 28°W, between 55° and 56°S. Much of the krill biomass was present in these more eastern regions of the Scotia Sea at the time of the CCAMLR 2000 Survey (Fig. 7A), suggesting that much of the krill biomass would, in time, have exited the Scotia Sea to the northeast. In the simulations these flows are seen as pulses of biomass that drift east, starting as a coherent stream along 35°W that extends from about 55° to 60°S, before taking a northward route around the South Sandwich Islands at about 30°W (Fig. 7D).

The krill around South Georgia were generally moved slowly to the west with the main flow of the ACC associated with the SACCF (Figs. 2 and 7). The krill were moved along and around the coast of South Georgia before being deflected northward out to the west of the island. At different periods in the simulation a plume of high krill biomass formed away from the island that streamed out along the main route of the SACCF, being deflected northward and then eastward with the main flow of the ACC. Krill encountered further to the west during the January survey were taken north and then east along this northern route of the SACCF. Krill close to the island are retained inshore although there is a general east to west flow. Krill in the vicinity of Bird Island (a small island to the northwest of South Georgia) were retained for the full 3-month period of the simulations.

3.4. Modifying effects of vertical migration

Lagrangian particle tracking shows the strong northward transport of particles in the very surface, wind-driven Ekman layer of the Scotia Sea (Fig. 8). Particles released in the surface layer of OCCAM (~10 m) in the Antarctic Peninsula and Elephant Island regions were carried rapidly northward across the ACC frontal zones and potentially out of the Southern Ocean over the Polar Front well to the west of South Georgia (Figs. 8A and 8B). Particles in deeper layers (to 245 m) were moved eastward with the general flow of the ACC associated with the SACCF and SBACC or with the WSC along the northern side of the Scotia Arc. The deepest particles entered the northern Weddell Sea by this route flowing around the southern side of the South Orkney Islands (Fig. 8A); however, this aspect of the flow may be an aspect of the OCCAM flows that is incorrect. The difference between the drift trajectories of particles released in the surface and deep layers farther east around the South Orkney Islands (Figs. 8C and 8D) did not result in such a marked divergence in flow as for those areas further west but the difference was still evident. Again, the surface particles would have a more northward component that can take material to the west of South Georgia, while the deeper particles pick up a more eastward flow that takes particles to the east of South Georgia. Particles in the depth-weighted mean field of the upper 245 m show trajectories intermediate between the surface and deep drifters but are more similar to the deep flow routes, reflecting the dominance of deeper flows in the mean field. The vertical migration scenario used, in which particles moved sinusoidally through the upper 245 m of the water column during a 24 h period, produced similar trajectories to the mean field flow routes, although they were further north and tended to be slower as shown by the shorter trajectories.

4. Discussion

4.1. Development of the krill distribution in the Scotia Sea during spring and early summer

The northward spread of krill in the Scotia Sea during spring is a crucial process in the operation of the regional ecosystem (Marr, 1962; Murphy et al., 1998). The large-scale dispersal of krill from southern shelf regions around the Antarctic Peninsula and the southern Scotia Arc makes the krill available to a wide range of predators whose

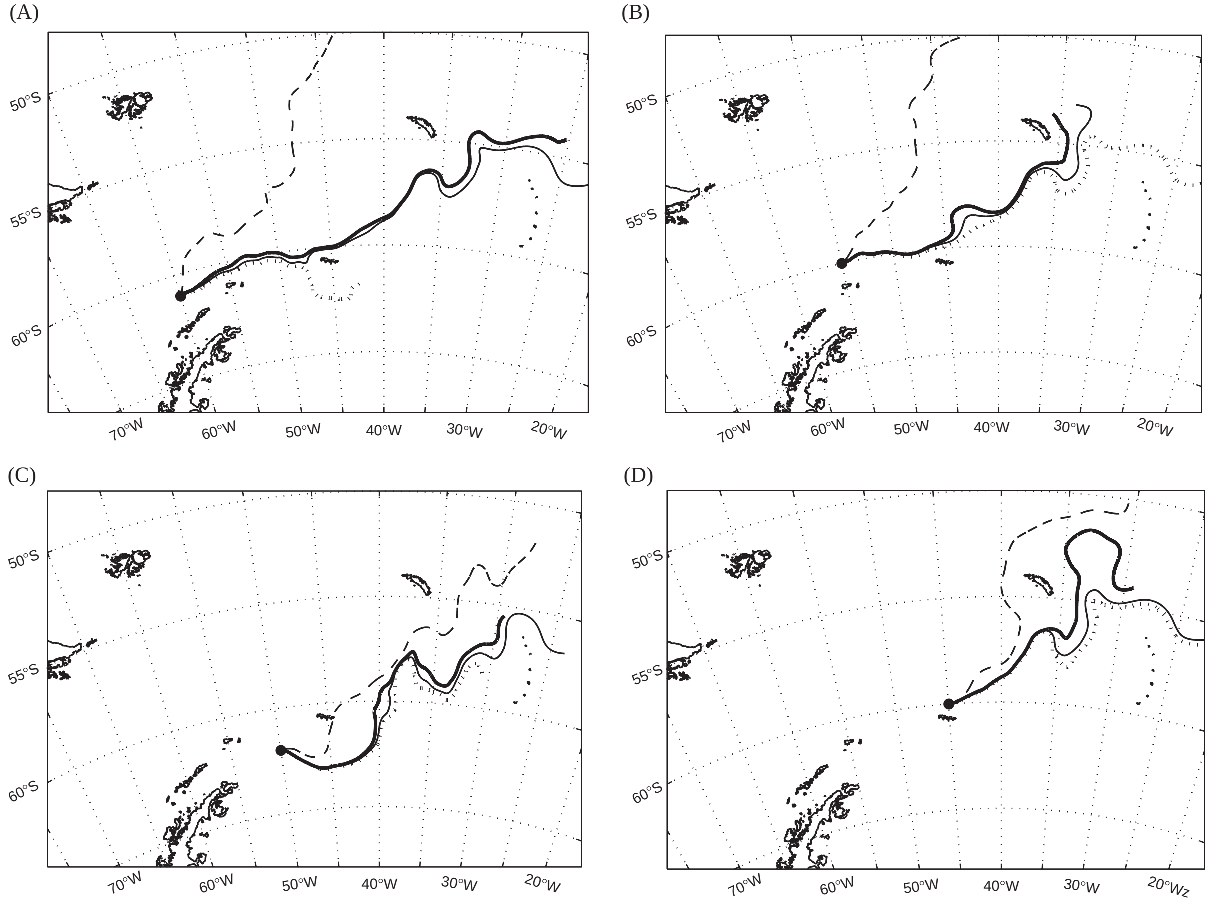

Fig. 8. Lagrangian particle tracks for particles released on 1 October 1999 at four sites in the survey region. Tracks are shown for single level drifters at the surface (~10 m dashed line) and at depth (~245 m dotted line) along with the track of a drifter through the depth-weighted mean field for the upper 245 m (solid line). The thick dark line shows the track of a vertically migrating particle that migrates over 245 m over 24 h following a simple sinusoidal migration.

foraging is constrained to more northern regions during the breeding season (Croxall et al., 1988). Understanding what determines the abundance of krill and the extent of the seasonal dispersal is crucial in attempts to examine the response of such large-scale ecosystems to change (Murphy et al., 1998). A question that continues to be asked in this regard is where do the krill come from that reach the northern Scotia Sea in areas such as South Georgia?

The particle and tracer tracking analyses reported in the current study support the view that the ACC is important in moving krill across northern areas of the Scotia Sea toward South Georgia during the spring (Hofmann et al., 1998; Murphy et al., 1998). However, a lack of krill in areas off-shelf between 60° and 40°W highlights that in this particular season there was no direct association of post-larval krill with the SACCF connecting the Antarctic Peninsula and South Georgia regions. Many of the krill were found across the fronts in areas to the east of the South Orkney Islands. To get to South Georgia these krill would have had to be transported northward across the SBACC into the SACCF. In these areas, where the fronts are not strongly topographically constrained, there will be much interaction between the frontal regions that may be important in transporting the krill northward (Brandon et al., 2004). Vertical differences may also be important; analyses of the vertical migration effects show that if the krill maintain a relatively shallow distribution (<50 m) they will tend to be transported northward across the fronts in the Ekman layer, a scenario illustrated by the tracks of the giant icebergs that passed through the region during the CCAMLR 2000 Survey (Brandon et al., 2004).

So the question of where post-larval krill found during summer in the northern Scotia Sea were spawned is not simple to answer. The most obvious track for moving krill from the west Antarctic Peninsula region toward the east is associated with the SACCF. However, most of the krill in the southern Scotia Sea during this study were observed south of the SBACC in WSC waters. In the analyses undertaken this view is complicated by the difficulty in identifying the exact positions of the ocean fronts in the coarse resolution CTD grid, and also because the OCCAM circulation field is deflected south in this region (Thorpe et al., 2004b; Brandon et al., 2004). The model analyses also indicate the potential for krill to be transported out of the northern Weddell Sea.

A general point that emerges in discussing the development of the summer krill distribution in the Scotia Sea is that tracking the krill in the high biomass regions back to their probable spring positions shows that many were associated with the sea-ice. The implication is that to track where the krill came from it is necessary to take account not only of the ocean circulation, but also the interaction of krill with the drifting sea-ice. The study has indicated a direct seasonal link between the pelagic krill distribution during summer and the sea-ice environment during the previous winter and spring (Murphy et al., 2004). The analyses suggest that most of the krill observed during the CCAMLR 2000 Survey would have been in sea-ice covered regions two to three months previously. Only the krill encountered in the northern Scotia Sea around South Georgia would have been outside the sea-ice zone at that time. Even the krill at South Georgia could have been in sea-ice covered regions 4–6 months previously, during the early winter period of July–August. These analyses support the view that much of the krill population observed in the Scotia Sea during summer is released into the Scotia Sea current flows during the spring retreat of the sea-ice zone (Marr, 1962; Mackintosh, 1972, 1973). This highlights that the krill-sea-ice interaction during spring will be crucial in determining the summer distribution of krill, and hence large-scale availability to predators.

Unfortunately there is little information about how krill interact with the sea-ice-ocean environment in these areas, but the available evidence about how krill utilize the sea-ice habitat indicates variation dependent on the characteristics of the sea-ice (Daly, 1990; Quetin and Ross, 1991). Sea ice provides a highly structured environment that shows marked variation in time and space (Eicken, 1992); so in some areas, such as the Weddell Sea, the occurrence of both annual and multi-year ice generates an environment that can be highly spatially structured over less than 1 metre to hundreds of metres. In other regions, such as the Antarctic Peninsula, annual ice that tends to be smooth can predominate, possibly making it a more homogeneous environment. As a strategy for obtaining food and predator avoidance in multi-year sea-ice regions krill often occur in close association with the ice, in brine channels and grazing on sea-ice algae growing on the sub-surface of ice floes (Marschall, 1988; Quetin and Ross, 1991; Siegel et al., 1990). Krill swarms also are found in the water column below the sea-ice (Brierley et al., 2002; Quetin and Ross, 1991; Sprong and Schalk, 1992), while in shelf areas that are sea-ice covered the krill may also be associated with bottom substrates and benthic communities (Gutt and Siegel, 1994).

This emphasizes that krill interactions with sea-ice habitats are likely to be complex and to vary through the season and between regions. This means that gaining a general understanding of the winter-spring-summer transition processes for krill emergence from under the ice will be difficult. This is further complicated by the lack of understanding of how the sea-ice and surface ocean interact in these regions. The sea-ice will modify the surface ocean characteristics in terms of temperature and salinity gradients such that the surface current fields will be very different to those expected when sea-ice is not present (Timmermann et al., 2002). This is likely to lead to enhanced current velocities along the ice edge in areas where the sea-ice drift is likely to be greatest (Timmermann et al., 2002). These processes will be crucial in determining the development of the summer krill distribution. A strong association of the krill with the sea-ice habitat would mean that the krill should show a predominantly ice-associated drift. Model-based analyses indicate that the mean direction of the ice drift in the southern Scotia Sea is to the northeast out of the northern Weddell Sea south of the South Orkney Islands, across the Scotia Sea toward the northern tip of the South Sandwich Islands (Timmermann et al., 2002, see their Fig. 8). So krill associated with the ice in winter and spring would have come from the northern Weddell Sea. The general pattern of sea-ice drift in the Weddell Sea further indicates that krill associated with the sea-ice will have come from further south within the Weddell Sea, being moved north and east along the eastern side of the Antarctic Peninsula. Such a view highlights the interconnected nature of the krill populations of the Southern Ocean with potentially multiple centers and regional connections (Marr, 1962). The Weddell Sea krill may be an important component of the large-scale krill population, with adult krill that are moved out of the area in spring returning to the central population regions during winter. This may be through interactions with the regional circulation in areas where there is a southward flow back toward the eastern Weddell Gyre regions, or with the sea-ice during periods of formation and retreat. To address this issue information on the detailed physical interactions between the ocean and sea-ice is required, and the krill interactions within and between these regimes. This should help develop a much better understanding of how krill respond to changing sea-ice cover during periods of ice retreat and formation.

In such a view of the system, with a dynamic ice cover fluctuating over the ocean currents, it becomes clear why simple associations between the large-scale distribution of krill and regional ocean fronts should not always be expected. Release of the krill into the pelagic regime during the spring period of sea-ice retreat means that their distribution in spring and summer will be a function of both the flow field and the historical association with the retreating ice edge. This historical aspect to the development of the distribution, combined with the importance of mesoscale variability, means that it will not be simple to specify that the krill are associated with a particular frontal system. Associations may be restricted, especially as a result of Ekman drift and enhanced current speeds that can act to aggregate and rapidly move particles across the central Scotia Sea (see Hofmann et al., 1998).

Much of the krill observed during the CCAMLR 2000 Survey in more southern regions in areas that would have been covered by winter sea-ice were in continental shelf regions. In these shallow regions complex physical and biological interactions will greatly affect the development of the krill distribution during spring and summer. In such areas retention rates (Murphy, 1995) may be much greater than indicated by the particle tracking with the broad resolution current data from the OCCAM model. The OCCAM model data cannot resolve the horizontal and vertical structure present in these areas. In such shallow regions fine-scale ocean interactions of the circulation with topography and local tidal effects will be important.

One of the key findings from the biological analyses of the krill distribution during the CCAMLR 2000 Survey was the occurrence of a high biomass of small (20–30 mm) krill in the eastern Scotia Sea (Siegel et al., 2004, see their Fig. 5). The distribution of these small krill did not extend continuously back to the Antarctic Peninsula region, rather the distribution of small krill extended to the south back into the northern Weddell Sea. The particle tracking analyses indicate that these small krill in the more southern regions would have emerged from under the ice in the southern-central Scotia Sea to the east of the South Orkney Islands, and may well have come from farther west in association with the WSC or out of the northern Weddell Sea associated with the main sea-ice drift. This suggests that the strong recruitment of these krill was not generated in the Antarctic Peninsula region but in the WSC along the Scotia Arc or in the Weddell Sea. However, the simulations show that some of these small krill in the more northern regions (green and dark blue squares in Fig. 4) could have been transported from the area north of the Antarctic Peninsula. The proposal that the year class originated in the Weddell Sea sector is consistent with the observation that recruitment indices in the Antarctic Peninsula region for the 1998/99 season were low indicating poor recruitment (Hewitt et al., 2004). Thus, these krill may have been produced from spawning to the east of the Antarctic Peninsula, possibly around the South Orkney Islands associated with the Scotia Arc, more generally in the WSC, or in the Weddell Sea.

These analyses indicate that there is likely to be sufficient exchange from west to east in krill stocks at the Antarctic Peninsula, in the southern Scotia Sea, and in the Weddell Sea that they effectively form a single population. This does not mean this single population is fully mixed, just that there may be sufficient exchange to maintain the population genetic homogeneity, but the center of production may vary right across the region from one year to the next. In different years the main center(s) of production of krill larvae and juveniles may vary across the region as a function of the regional environmental conditions. There are also known to be pathways that show reverse flows from east to west into the Bransfield Strait from the shelf regions in the western Weddell Sea (von Gyldenfeldt et al., 2002), so krill can be mixed back into more western regions further maintaining the regional population. Such a scenario would appear to give the regional population the capacity to overcome local fluctuations in environmental conditions from 1 year to the next.

The model analyses also indicated that during 1999/2000 much of the krill exited out to the east of the Scotia Sea away from South Georgia, probably in Weddell Sea waters south of the SBACC. These different routes of transport may indicate that South Georgia is generally more dependent on recruitment from the Antarctic Peninsula region, which may be why length-frequency analyses indicate that krill year-class strength tends to be similar in the Antarctic Peninsula and South Georgia regions (Reid et al., 2002).

Data available on the distribution of larval krill during the CCAMLR 2000 Survey (Siegel et al., 2004; Ward et al., 2004) do not allow definitive statements about the region where spawning occurred. Lagrangian analyses indicate that krill larvae observed in the most southerly regions during January (south of 60°S) could have come from under the ice close to where they were observed or could have emerged from under the ice in the WSC or northern Weddell Sea as late as November or December. Larvae observed in more northern areas of the Scotia Sea may have been produced in a similar area around the South Orkney Islands in association with the retreating ice edge. Such a scenario would be likely if the early krill developmental stages spend a significant part of the day in the very surface layers (<50 m) where the currents have a strong northward component associated with the wind-driven layer. Alternatively, the krill larvae in the more northern regions may have been generated in areas further west closer to the Antarctic Peninsula region in areas of retreating sea-ice during spring and then have been moved eastward in association with the SACCF and SBACC. The potential also exists for enhanced eastward transport rates near the ice edge as a result of ice-edge current jets, which could generate movement over relatively large distances, further complicating the interpretation of the observed distributions.

4.2. Development of the krill distribution in the Scotia Sea during summer

A key question in relation to the krill distribution in the Scotia Sea concerns the positions of the exit routes for krill during summer. This will be important in understanding whether there is the potential for the krill to return to the main spawning regions to contribute to future generations in the area. This in turn will be crucial in the dynamics of the regional population with any feedbacks having a major effect on long-term dynamics.

The Eulerian runs indicate that during the 1999/2000 season a lot of the krill in the Scotia Sea during the CCAMLR 2000 Survey would have been transported out of the region around the north of the South Sandwich Islands. Some of these krill may have become entrained in these island regions due to mesoscale shelf effects and behavioral interactions, but the model runs indicate that this may have been a major flow route during this season. These regions are known to contain large predator colonies, and such a flow route may help explain how the colonies are maintained (Convey et al., 1999). Much of the flow would have been associated with the SBACC and regions to the south in Weddell Sea water. Such a flow around the South Sandwich Islands will tend to be deflected south in the main flow to the east of the islands and so provide a route for potential connection back into the eastern Weddell Gyre region. A return of krill to the south, as suggested by Marr (1962), has important implications for understanding long-term krill population dynamics owing to the population feedback effects (Murphy, 1995; Murphy et al., 2004).

The model analyses indicate a strong sensitivity in the particle flow tracks in the central Scotia Sea, with some of the krill being transported to South Georgia while krill slightly further east would be moved eastward to pass to the north of the South Sandwich Islands. As already noted, these areas are well to the north of the WSC and are areas of intense eddy activity where the fronts are not topographically constrained. To what extent this is a general feature or a single-year effect generated by the wind and circulation conditions of the 1999/2000 season is unclear. The strong eastward flow observed during 1999/2000 may have been the result of the particular conditions observed during the season. Such a view would support suggestions that the wind and ocean circulation conditions may be a strong determinant of the major flow routes in different years and hence crucial in generating the observed regional interannual variation (Fedulov et al., 1996; Mackintosh, 1972, 1973; Murphy et al., 1998; Priddle et al., 1988). The potential for physically driven interannual variability in krill transport to determine large-scale changes in distribution will be a valuable focus for further model studies (Thorpe et al., 2002, 2004a).

4.3. Krill as passive tracers, the importance of behavior and swimming

An assumption of the modeling analysis is that at least in the main open-ocean regions the krill are transported largely passively in the main flow field. While maximum swim speeds of 8 body lengths per second ($\sim$25–48 $cm\,s^{-1}$) have been measured (Kils, 1979), a sustainable swimming speed is thought to be much lower, at about 13 $cm\,s^{-1}$ (Kils, 1981). In areas where the current velocities are strong and consistent, horizontally and vertically, and in open-ocean regions, the assumption of passive transport is reasonable. In areas where current velocities are low and variable, or in regions of marked vertical shear, krill swimming is likely to be an important aspect in the development of the krill distribution. However, there is little evidence of any marked spatial migratory behavior in areas away from the shelf regions. Some studies have apparently noted directed swimming migrations of krill, as opposed to localized movement (Kanda et al., 1982; Sprong and Schalk, 1992). However, detecting directed movement of krill aggregations in areas where there is marked mesoscale variation in the current field, such as at ice edges, requires simultaneous measurements of the krill movement and the current field over sufficiently long periods to show differential and directed movement. Any seasonal migratory behavior, such as a southward migration during late summer, could have a major impact on distribution, but there is no evidence of such behavior. Therefore, the simplest view of distribution changes at this stage can only consider local behavioral responses that may have a larger scale impact such as vertical migration.

The analysis in this study shows that behaviorally driven diurnal vertical migration of krill produces very different drift trajectories and will be important in the Scotia Sea. The crucial aspect is the amount of time the krill spend in the very surface waters, which have a strong northward velocity component. The results show that the horizontal and vertical positions of krill in the central Scotia Sea generate very different outcomes in terms of flow routes. The central Scotia Sea seems to be a particularly sensitive region for determining the krill trajectories. Depending on geographical location and vertical position, krill can be transported to the west of South Georgia, can be moved around the east and along the north coast of the island, or can be transported east, out of the Scotia Sea, missing South Georgia completely. The OCCAM model data do not allow further resolution of such an effect because the main wind-driven impacts are largely confined to the surface (20 m thick) layer so that the simulations give an unrealistic view of the importance of the surface northward layer.

The simulations cannot account for a directed cross-shelf migration of the form that krill are thought to undertake in the Antarctic Peninsula region (e.g., Trathan et al., 1993). Krill that occur in inshore regions of the Antarctic Peninsula and then migrate across the shelf and the main direction of flow would produce very different trajectories. These krill also may exploit the strong vertical structure in these regions, possibly vertically migrating to depth into the upwelling Circumpolar Deep Water (Prezelin et al., 2000), which will have an on-shelf direction to the flow and would return the adults back toward more inshore regions. Given the potential for strong behavioral effects due to directed swimming, horizontally or vertically, krill could be retained for very long periods in habitats where primary production may be high and thus favorable for krill growth and development (Siegel, 1988).

It is interesting to note from the Eulerian simulations that flow interaction with the krill distribution generates plumes of high krill biomass away from the island groups at certain times. This highlights that passive tracers in the flow field can appear to generate enhanced levels of plankton as plumes downstream of the island groups. This is likely to be important in generating the large-scale distributions of other plankton, including phytoplankton, which also show rapid population growth.

4.4. Future developments

Developing coupled model analyses of krill growth and development with the environment is already underway (Fach et al., 2002). For future developments of the present study, the environment will need to include the physical characteristics (current speeds, directions, and temperature) and food availability based on ocean color imagery from CZCS and SeaWiFS or through coupling with lower trophic level models. The present Eulerian model runs did not include growth or mortality processes, which are known to be spatially and seasonally variable (Murphy and Reid, 2001; Reid et al., 2002), so these will need to be included and are likely to markedly affect the development of the biomass distribution during summer. Linking to the time-varying sea-ice distribution as determined from satellite data also will be useful although major advances will be possible when realistic coupled ice-ocean models are operational. For a krill population operating over coastal and ocean systems in areas of steep bathymetry, models will be required that include nested higher resolution local models. The overall emphasis of future studies will need to consider how the entire krill life cycle interacts with physical advection and retention to maintain the major krill populations. Thus it will be important to include reproduction and the early life history stages. In particular, the extent to which krill transported away from the southern Scotia Sea can later produce viable offspring that return to the main spawning regions and so contribute to future generations needs to be determined.

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